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A STUDY OF ASYMMETRY, AS DEVELOPED IN THE GENERA AND FAMILIES OF RECENT CRINOIDS

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PREFACE

IN the animal kingdom there are few, if any, forms which can be properly described as perfectly symmetrical, either from a bilateral or a radial standard. We have, however, become accustomed to refer to many types as "asymmetrical." In the sense in which we employ this word we do not intend to convey the meaning that these types alone of their respective classes depart from true bilateral or radial symmetry, but rather to indicate that they exhibit more asymmetry than the maximum contemplated in our generalized concept of, or arbitrary standard for, those classes.

Thus we readily recognize and confess the asymmetry in the skull of the narwhal (*Monodon*) with its single greatly elongated and twisted incisor, and the asymmetry in the bones in the skull of the whales, while at the same time we commonly consider man to be symmetrical, though careful measurement shows the right arm and

hand to be larger than the left, and the left leg and foot to be larger than the right.

It is clear, therefore, that in dealing with asymmetry in any group we must work inward from the most asymmetrical types toward the least asymmetrical, arbitrarily erecting a barrier between what we call asymmetry and what we are pleased to consider as "symmetry" at any point we choose.

Asymmetry—that is to say the maximum departure from perfect bilateral or radial symmetry—appears to follow certain definite lines wherever it appears, quite regardless of the type of animal, or the form, in which it is manifested.

In the following pages we shall consider the wider variations from the typical pentamerous symmetry among the recent crinoids, which is phylogenetically most extensively developed at the consummation of the phylogenetic lines, and physico-economically most extensively developed in the situations most unsuited to crinoidal existence, particularly in the very warm water of the East Indian and north Australian littoral, and the very cold water of the Antarctic regions and the deep abysses of the oceans, and is least evident among phylogenetically conservative types, and in the situations which appear to be best suited for crinoid life.

As an indication of the possible fundamental importance of the light thrown on the study of asymmetry by an examination of the data offered by the recent crinoids, it may be noticed and borne in mind that among the mammals the phylogenetically aberrant asymmetrical narwhal (*Monodon*) is exclusively arctic; the phylogenetically aberrant asymmetrical whales occupy a habitat very aberrant for the class; and the anthropoid apes, which are pronouncedly right or left handed, live in very warm regions; that among the birds the curious crook-billed plover (*Anarhynchus*), with the beak twisted to the right and one side of the body lighter in color than the other, occurs only in New Zealand, the home of many phyloge-

netic oddities; the hornbill *Rhinoplax*, with an asymmetrical tail, further peculiar in having a solid casque, an elongate central rectrix, and a naked patch on the back extending to the sides of the head, is found in the warm Malayan region; the crossbills (*Loxia*), with the tips of the mandibles crossed and a corresponding distortion in the bones of the head are all subarctic or cold temperate forms; and the owls with one ear greatly larger than the other, so far as has been determined are, like the crossbills, birds of the colder regions; and that among the fishes and similar types the very asymmetrical *Anableps* lives in the warm tropical littoral, while the flatfishes (Pleuronectidæ) are chiefly developed in the warm tropical littoral, and in cold and shallow water, and the asymmetrical forms of "Amphioxus" (using the term in its broadest sense) occur in warm and shallow water.

Further it is interesting to recall that animals under domestication—that is, living under conditions which typically lead to a more or less degenerate diversity in form and color—commonly develop asymmetry of action which, though usually occurring in the form of individual variation, may become very marked as in the case of the Japanese waltzing mice, as well as pronounced, though irregular and sporadic, asymmetry in color pattern, dentition, and other features.

More or less pronounced asymmetry undoubtedly exists in many types in which up to now it has been overlooked, and the conclusions reached in the present paper may be modified somewhat when a better knowledge of the subject is attained; but on the other hand it is scarcely probable that many instances of marked asymmetry have escaped the notice of naturalists.

THE DIFFERENT TYPES OF CRINOIDAL ASYMMETRY

In the great majority of the recent crinoids the body is almost perfectly pentamerous, being composed of five similar sectors. The presence of a small muscular cone in the posterior interradius, at the summit of which is

the posterior opening of the spiral digestive tube, gives the only visible indication of a departure from true pentamerous symmetry.

In certain types, however, a more or less marked deviation from the characteristic symmetry occurs. This deviation follows four different lines:

1. A rearrangement of the five primary groove trunks upon the disk whereby (*a*) the left posterior increases in size and gives off more branches than any of the others; (*b*) as a result of the anterior migration of the mouth, the two posterior become much longer and the anterior much shorter than the others and a condition of bilateral symmetry is attained; (*c*) correlated with the anterior migration of the mouth, all of the primary groove trunks become merged into a horse-shoe shaped ring which skirts the lateral and anterior borders of the disk, giving off branches to the arms, the mouth being in the right center of the ring so that the ambulacra on the left are more developed than those on the right, or the ambulacra leading to the left posterior arm disappearing altogether so that the ambulacra on the right are more developed than those on the left;

2. A dwarfing, or an overdevelopment, of the left posterior, more rarely of both, posterior radials with their post-radial series;

3. The intercalation of additional radials and post-radial series which alternate with the original five, and the associated dropping out of one of the five radials; and

4. The suppression of two of the primarily five basals.

THE ASYMMETRICAL CRINOIDS

In the following list are given all the families and genera of recent crinoids which include asymmetrical species.

After the families the bathymetrical and thermal ranges are given, and after the genera the bathymetrical range.

Certain families are represented in the warm littoral

water of the Malayan region and northern Australia, but the highest actual temperature record is considerably less than the temperature of this water; in these cases the temperature 80.5° is given after the ascertained maximum as more nearly representing the true maximum.

Of the nine families the four in which asymmetry is most markedly developed are marked with an asterisk (*); and of the twenty-seven genera the sixteen which include the most notably asymmetrical species are similarly distinguished.

	Depth (Fathoms)	Temperature (F.)
Capillasterinæ	0-830	44.5-78.5 (80.5)
<i>Ccomatella</i>	0-106	
<i>Neocomatella</i>	10-830	
<i>Paleocomatella</i>	140-153	
<i>Capillaster</i>	0-160	
<i>Nemaster</i>	0-194	
<i>Comissia</i>	0-100	
<i>Leptonemaster</i>	42-163	
Comactiniinæ	0-288	62.0-71.9 (80.5)
* <i>Comatula</i>	0-160	
<i>Comatulella</i>	0-10	
<i>Cominia</i>	0-288	
<i>Comactinia</i>	0-262	
*Comasterinæ	0-140	52.3-80.0 (80.5)
* <i>Comaster</i>	0-95	
* <i>Comantheria</i>	0-83	
* <i>Comanthina</i>	0-42	
* <i>Comanthus</i>	0-140	
Heliometrinæ	2-1,600	28.7-60.5
* <i>Promachocrinus</i>	10-222	28.7
Pentametrocrinidæ	103-1,800	33.5-60.6
* <i>Thaumatoerinus</i>	361-1,800	
*Apiocrinidæ	565-940	36.7-38.1
* <i>Proisocrinus</i>	940	
* <i>Carpenterocrinus</i>	565	
Bourguetierinidæ	62-2,690	29.1-70.7
* <i>Rhizocrinus</i>	77-1,300	32.2-48.7
<i>Monachocrinus</i>	687-2,419	37.4-40.0
*Holopodidæ	5-120	71.0
* <i>Holopus</i>	5-120	
*Plicatocrinidæ	266-2,575	31.1-43.9
* <i>Calamocrinus</i>	392-782	
* <i>Ptilocrinus</i>	266-2,485	
* <i>Hyocrinus</i>	1,600-2,575	
* <i>Gephyrocrinus</i>	992-1,103	
* <i>Thalassocrinus</i>	1,262-2,325	

THE PHYLOGENETIC DISTRIBUTION OF ASYMMETRY

The phylogenetic distribution of the asymmetry among the recent crinoids is very interesting.

Asymmetry is almost universal in the comatulid family Comasteridæ, which includes the most specialized of all recent forms; in this family the first and second types occur, though the latter is much less common.

Asymmetry is characteristic of the genus *Promachocrinus*, which is probably rightly considered as the most specialized genus in the subfamily Heliometrinæ, the largest and most universally distributed subfamily of the at present dominant family Antedonidæ; in the genus *Promachocrinus* the first and third types occur.

Asymmetry is equally characteristic of the genus *Thaumatoocrinus*, the most specialized genus of the family Pentametrocrinidæ; in this genus the third type is found.

Asymmetry exists in all of the genera of the Plicatocrinidæ, which includes the last highly specialized exponents of the ancient order Inadunata, which flourished from the Ordovician to the Carboniferous, with one family extending into the Permian and Trias and another (the present family) appearing in the Jura; in the Plicatocrinidæ the first, second and fourth types occur in recent genera, while the third is also found in fossil genera.

Asymmetry is characteristic of both of the recent genera of Apiocrinidæ, which are the most specialized genera in the family; in these the second type occurs.

Asymmetry of the second type is characteristic of the only recent genus of the Holopodidæ.

Asymmetry characterizes both of the species of *Rhizocrinus*—which is at least as highly specialized as any of the genera of the Bourgueticrinidæ—existing in the present seas, and one of the species of *Monachocrinus*, a genus of which the exact phylogenetic position is uncertain, although it is probably on a par with *Rhizocrinus*; in these the third type occurs.

In the following list the recent asymmetrical types are

given in the order of the extent of their departure from the normal pentamerous symmetry:

Plicatocrinidæ:	Asymmetry of Types 1, 2, (3) and 4.
Comasteridæ:	Asymmetry of Types 1 and 2.
<i>Promachocrinus</i> :	Asymmetry of Types 1 and 3.
Apiocrinidæ:	Asymmetry of Type 2.
Holopodidæ:	Asymmetry of Type 2.
<i>Thaumatocrinus</i> :	Asymmetry of Type 3.
<i>Rhizocrinus</i> :	Asymmetry of Type 3.
<i>Monachocrinus</i> :	Asymmetry of Type 3.

The asymmetry of the Comasteridæ is considered more fundamental than that of *Promachocrinus* for the reason that it is characteristic of practically the entire family, and also because it results in a much greater degree of irregularity. It is interesting to note that asymmetry of Type 3 is not uncommon among the Comasteridæ, in the form of individual variation.

The asymmetry of the Apiocrinidæ and Holopodidæ is considered more fundamental than that of the genus *Thaumatocrinus* for the reason that it affects the entire family, at the same time inducing a greater departure from the normal form.

The asymmetry of *Rhizocrinus* is considered less fundamental than that of *Thaumatocrinus* because, though affecting all of the species, exactly as in *Thaumatocrinus*, it is less extensively developed.

The asymmetry of *Monachocrinus* affects only one of the seven species of the genus.

Briefly stated, it appears that, no matter in what form it may manifest itself, metameric asymmetry in the recent crinoids is an attribute of the most specialized types in the groups in which it occurs.

From the conditions in the Plicatocrinidæ, the last remnants of the once abundant Inadunata, it would appear that asymmetry is an attribute of phylogenetically decadent types—types in which type senescence has so far advanced as to inhibit the normal course of development.

THE GEOGRAPHICAL DISTRIBUTION OF ASYMMETRY

The geographical distribution of asymmetry is as interesting as the phylogenetical distribution.

Although occurring everywhere except in the Arctic Ocean and in the Mediterranean, Bering, Okhotsk and Japan seas, asymmetrical types are most frequent and most highly developed (1) in warm shallow water from southern Japan southward throughout the Malay Archipelago to northern Australia and westward to Ceylon, and (2) in the Antarctic and in the cold abysses.

Though present among species inhabiting the west Atlantic from North Carolina to Brazil, and characteristic of many forms living at intermediate depths in the western Pacific and in the Indian Oceans, in these it is never more than slightly developed, even though they be very closely related to types in which it is, in other situations, carried to an extreme.

Depth (Fathoms)	Number of Asymmetrical Genera	Number of Symmetrical Genera	Per Cent. of the Latter Represented by the Former
0-50	16	50	32%
50-100	15	53	28
100-150	13	51	25
150-200	10	44	22
200-250	5	39	13
250-300	5	34	14
300-350	3	30	10
350-400	4	32	12
400-450	5	29	17
450-500	5	27	18
500-550	5	26	19
550-600	6	26	23
600-650	5	26	19
650-700	6	22	27
700-750	6	22	27
750-800	6	18	33
800-850	5	18	28
850-900	4	18	22
900-950	5	19	26
950-1,000	5	16	31
1,000-1,100	5	16	31
1,100-1,200	5	12	41
1,200-1,300	5	9	55
1,300-1,400	4	9	44
1,400-1,500	4	7	57
1,500-1,600	4	7	57
1,600-1,700	5	3	166
1,700-1,800	5	3	166
1,800-1,900	4	3	133
1,900-2,000	4	3	133
2,000-2,500	4	3	133
2,500-3,000	1	3	33

In short, though almost universal, occurring every-

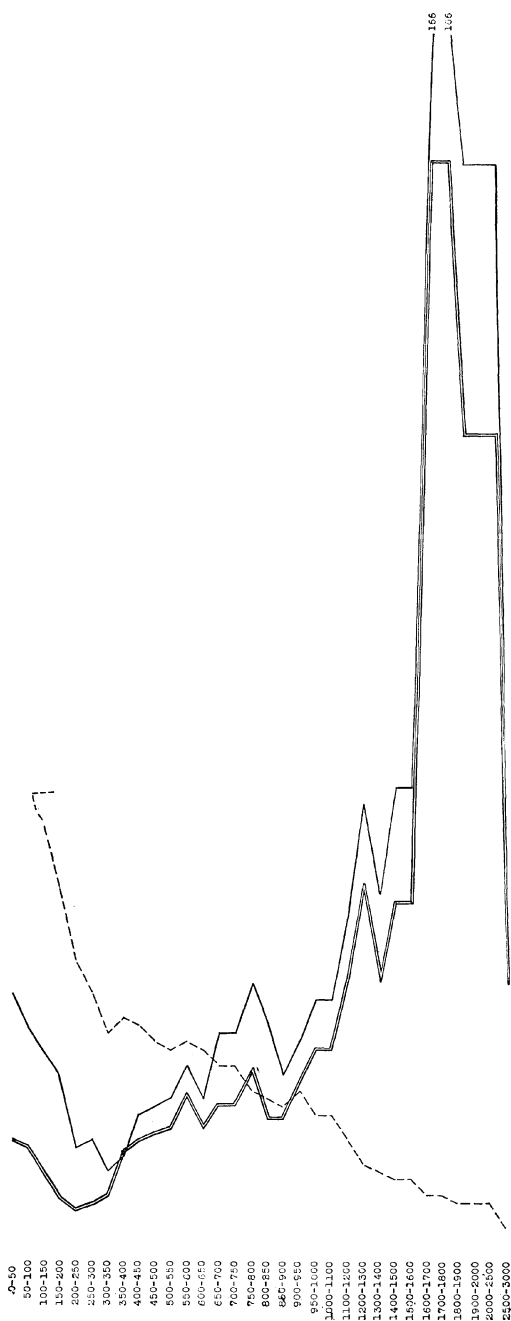


FIG. 1. The Relation between the Genera with and without Asymmetrical Species at Different Depths (—), with very Asymmetrical and without Asymmetrical Species at Different Depths (==), and the Decrease in the Number of Genera with Depth, expressed in Percentages of the Total Number (- - -).

where except in inland seas, asymmetry is especially developed in the warm waters of the eastern tropics, particularly in the Malayan region and in northern Australia, and in the Antarctic and the cold abysses.

BATHYMETRICAL DISTRIBUTION OF THE ASYMMETRICAL CRINOIDS

The number of genera of recent crinoids including asymmetrical species, the number of genera including

Depth (Fathoms)	Number of Asymmetrical Genera Which Are Marked *	Number of Symmetrical Genera	Per Cent. of the Latter Represented by the Former
0-50	7	50	14.0
50-100	7	53	13.2
100-150	5	51	9.8
150-200	3	44	6.8
200-250	2	39	5.1
250-300	2	34	5.8
300-350	2	30	6.6
350-400	4	32	12.5
400-450	4	29	13.8
450-500	4	27	14.8
500-550	4	26	15.4
550-600	5	26	19.2
600-650	4	26	15.4
650-700	4	22	18.1
700-750	4	22	18.1
750-800	4	18	22.2
800-850	3	18	16.6
850-900	3	18	16.6
900-950	4	19	21.0
950-1,000	4	16	25.0
1,000-1,100	4	16	25.0
1,100-1,200	4	12	33.3
1,200-1,300	4	9	44.4
1,300-1,400	3	9	33.3
1,400-1,500	3	7	42.8
1,500-1,600	3	7	42.8
1,600-1,700	4	3	133.3
1,700-1,800	4	3	133.3
1,800-1,900	3	3	100.0
1,900-2,000	4	3	100.0
2,000-2,500	3	3	100.0
2,500-3,000	1	3	33.3

only symmetrical species, and the percentage of the number of symmetrical genera represented by the number of asymmetrical genera at different depths are given in the table on page 528 and shown in Fig. 1.

Considering the percentages only, these may be re-grouped as follows:

0- 200	27
200- 650	16
650-1,100	28
1,100-3,000	92

Considering only the genera marked with an asterisk (*) we find the representation at different depths given in the table on page 530 and in Fig. 1.

Considering the percentages only, these may be re-grouped, as follows:

0- 100	13.6
100- 350	6.8
350- 900	16.6
900-3,000	61.8

The number of families of recent crinoids including asymmetrical species, the number of families including only symmetrical species, and the percentage of the number of families including only symmetrical species represented by the number of families including asymmetrical species at different depths, are shown in the table on page 533 and in Fig. 2.

The proportion of the genera including asymmetrical species to those composed entirely of symmetrical species, about one third between the shore line and 50 fathoms, decreases to a minimum of one tenth at from 300 to 350 fathoms, and then increases, with greater and greater rapidity, to 1,600 fathoms and below.

It is everywhere less than one quarter between 100 and 650 fathoms. Thus it is evident that the genera including asymmetrical species are chiefly developed in shallow water, and in deep water, and are least developed in water of intermediate depth.

Taking the ocean as a whole, the temperature at 100 fathoms is 60.7° , and at 650 fathoms 38.6° ; the optimum temperature for the recent crinoids appears to be between 50° and 65° ; when we remember that most of the asymmetrical species, and all of the most asymmetrical ones, in the genera which give us our numbers for 0-50 and for 50-100 fathoms, are confined to a littoral belt of scarcely more than 50 fathoms, it becomes at once evident that asymmetry among the crinoids is developed chiefly in

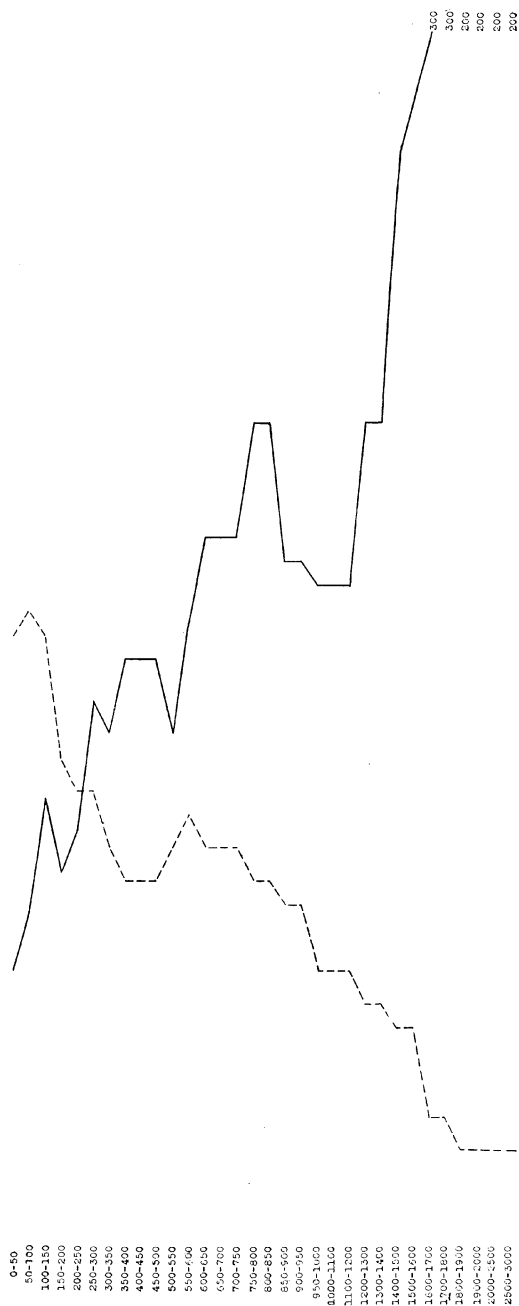


FIG. 2. The Proportion of Families with and without Asymmetrical Species at Different Depths (—), and the Percentage of the Total Number of Crinoid Families represented at Different Depths (---).

Depth (Fathoms)	Number of Asymmetrical Families	The Families Marked with an *	Number of Symmetrical Families	Per Cent. of Sym- metrical Families Represented by the Asymmet- rical
0-50	5	2	15	33
50-100	6	2	15	40
100-150	7	2	13	54
150-200	5	0	11	45
200-250	5	0	10	50
250-300	6	0	9	66
300-350	5	0	8	62
350-400	5	0	7	71
400-450	5	0	7	71
450-500	5	0	7	71
500-550	5	0	8	62
550-600	6	1	8	75
600-650	6	1	7	86
650-700	6	1	7	86
700-750	6	1	7	86
750-800	6	1	6	100
800-850	6	1	6	100
850-900	5	1	6	83
900-950	5	1	6	83
950-1,000	4	0	5	80
1,000-1,100	4	0	5	80
1,100-1,200	4	0	5	80
1,200-1,300	4	0	4	100
1,300-1,400	4	0	4	100
1,400-1,500	4	0	3	133
1,500-1,600	4	0	3	133
1,600-1,700	3	0	1	300
1,700-1,800	3	0	1	300
1,800-1,900	2	0	1	200
1,900-2,000	2	0	1	200
1,900-2,000	2	0	1	200
2,000-2,500	2	0	1	200
2,500-3,000	2	0	1	200

water above and below the optimum, and least at and just below the optimum temperature.

Considering only the genera marked with an asterisk (*), that is, the genera with the most highly developed asymmetry, we find the same general facts emphasized as in the case of all the genera including asymmetrical forms; but here the minimum is between 50 and 400 fathoms instead of between 100 and 650 fathoms. The temperature at 400 fathoms is 41.8° . This approximation of the minimum to the zone of optimum temperature when only the most asymmetrical types are considered strengthens the hypothesis that the zone of optimum temperature really represents the zone of least-developed asymmetry.

Comparing the proportionate abundance of asymmetrical genera at different depths with the frequency of all the genera expressed as percentages of the total, we find that the former decreases while the latter increases to 50–100 fathoms; from this point the two run roughly parallel to 300–350 fathoms, after which the former increases with progressively greater rapidity, while the latter decreases steadily and gradually to 3,000 fathoms; the two cross each other between 600 and 700 fathoms.

The proportion of the families including asymmetrical species to those composed entirely of symmetrical species increases from one third at 0–50 fathoms to three times as many at 1,600 fathoms and twice as many at 1,900 fathoms and over. The increase, though irregular—largely as a result of the small numbers involved at the greater depths—is constant.

The number of families at different depths, expressed as percentages of the total number, increases from 0–50 to 50–100 fathoms, and then decreases to 1,800 fathoms and beyond. Except for a minimum between 350 and 500 fathoms the decrease is fairly regular.

The two lines cross between 200 and 300 fathoms.

The reversal of the direction of the line representing the frequency of the families including asymmetrical species as a percentage of the number of the families not including asymmetrical species at different depths, as compared with the line representing the frequency of the families at different depths expressed as percentages of the total number, indicates that the less favorable the environment for crinoids as a whole the greater becomes the proportion of asymmetrical forms.

In the proportion of genera including asymmetrical species to those composed entirely of symmetrical species we find a minimum between 100 and 650 fathoms or, considering only the most markedly asymmetrical types, between 50 and 400 fathoms, the numbers above 100 (or 50) fathoms and below 650 (or 400) fathoms being greater.

Considering families in the same light we appear to

have an increase between 350 and 500 fathoms—that is, more or less coinciding with this minimum.

In the frequency of families at different depths expressed as percentages of the total number we notice a minimum between 350 and 500 fathoms which reaches a point not again touched until 750–800 fathoms and beyond.

This indicates the occurrence here of a proportionately large number of families including asymmetrical species, but at the same time a proportionately small number of genera including asymmetrical species within those families.

THERMAL DISTRIBUTION OF THE ASYMMETRICAL CRINOIDS

In examining the thermal distribution of asymmetry among the recent crinoids we find it advisable to employ family instead of generic units, for the reason that our records are insufficient to furnish us with even approximate thermal ranges for many of the individual genera, though in most cases these may be estimated with reasonable exactness. The records for the crinoids of the deeper water are far more satisfactory than the records for the crinoids of the littoral, and this is very fortunate, for it justifies us in assigning a temperature of 65° and over to a number of species and genera which are of great importance in the present study.

In considering asymmetry in relation to temperature by family units it must constantly be borne in mind that, whereas certain families (Capillasterinæ, Comactiniinæ and Comasterinæ) extend from the warm littoral into moderately deep water with a relatively low temperature, the asymmetry among their component genera and species is strongly marked only in very shallow water of high temperature, and is only slightly marked—indeed not infrequently entirely absent, as in *Comatilia*—in genera and species inhabiting deep and cold water.

Thus through a study of family units the amount of asymmetry shown at intermediate temperatures is really exaggerated, and appears in its relation to the higher

and to the lower temperatures considerably greater than it really is.

In the subfamily Heliometrinæ, the largest and most widely distributed subfamily of the Antedonidæ, which itself is the dominant crinoid family of the present seas, the range of temperature is very great; but as only one out of the ten genera of the Heliometrinæ is asymmetrical it has seemed sufficient to consider and to tabulate the temperature of this genus (*Promachocrinus*) alone.

The frequency of the families including asymmetrical crinoids at different temperatures is as follows:

85-80°	4
80-75	4
75-70	4
70-65	3
<hr/>	
65-60	4
60-55	3
55-50	3
<hr/>	
50-45	3
45-40	4
40-35	5
35-30	4
30-25	1

These frequencies fall into the following groups:

Below 30°	1
30-45	4.3
45-65	3.2
65-85	3.7

or,

Below 30°	1
30-45	4.3
45-70	3.2
70-85	4.0

Considering the zone of optimum temperature (50°-65°) in contrast to the temperatures above and below, and omitting the exceptionally low temperatures below 30°, we have:

30-55°	3.8
50-65	3.3
65-80	4.0

Bearing in mind always that the frequency between the warm littoral and the cold abyssal temperatures is exaggerated because of the segregation in the warm littoral zone of the most asymmetrical genera and species in many of the families inhabiting intermediate temperatures, it is clear that asymmetry is least developed at the optimum temperature for crinoid life, and most developed in temperatures which are phylogenetically too warm or too cold.

This agrees perfectly with what we found from an examination of the bathymetrical distribution of asymmetry.

A comparison between the frequency of the families of crinoids represented in the recent seas, including only symmetrical species, given in the actual numbers and also as percentages of the total numbers, and the frequency of the families including asymmetrical species, given in the same way, follows (Fig. 3):

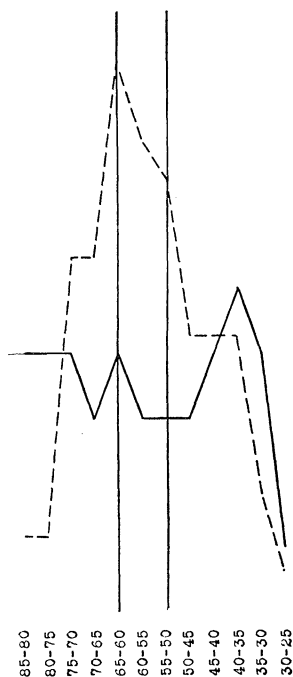


FIG. 3. Frequency at Different Temperatures of the Families including Asymmetrical Species (—), and those including Symmetrical Species only (---).

Temperature (Fahrenheit)	Families with Symmetrical Species Only	Per Cent. of Total	Families with Asymmetrical Species	Per Cent. of Total
85°-80°	2	13	4	44
80 -75	2	13	4	44
75 -70	9	60	4	44
70 -65	9	60	3	33
65 -60	14	93	4	44
60 -55	12	80	3	33
55 -50	11	73	3	33
50 -45	7	47	3	33
45 -40	7	47	4	44
40 -35	7	47	5	55
35 -30	3	20	4	44
30 -25	1	7	1	11

THE ASYMMETRICAL FEATURES IN DETAIL

In the following list are given the four types of asymmetry occurring in the recent crinoids, with their geographical distribution and the genera in which they are found.

1. *Disk Not Radially Symmetrical*

Geographical Distribution.—Southern Japan southward to Samoa, Fiji and southern Australia, thence west-

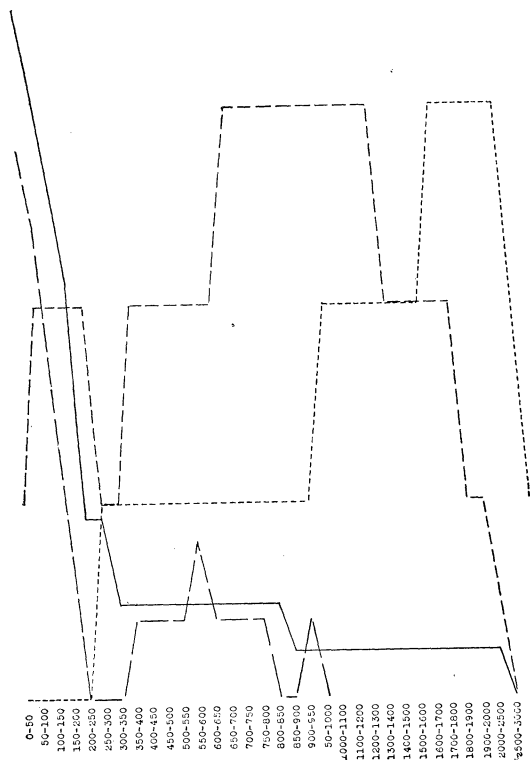


FIG. 4. Frequency at Different Depths of the Genera with Asymmetrical Disks (—), the Genera with One or More Rays Dwarfed or Enlarged (— — —), the Genera with Six to Ten Rays (- - - -), and the Genera with Three Basals (-), expressed as Percentages of the Total Number in Each Class.

ward to east Africa, from the Red Sea to the Cape; north-western Africa and southwestern Europe (in moderately deep water), and from South Carolina to Brazil; antarctic regions, littoral to abyssal, and northward along the

eastern shores of the Pacific (in deep water) to British Columbia.

This character is most strongly marked in the shallow water from the Marshall Islands and New Caledonia through the Malay Archipelago and along the northern coasts of Australia, and thence westward to Ceylon; and again in the antarctic regions and the abysses of the east Pacific.

Systematic Distribution.—

	Capillasterinæ
<i>Comatella</i>	<i>Capillaster</i>
<i>Neocomatella</i>	<i>Nemaster</i>
<i>Palæocomatella</i>	<i>Comissia</i>
	<i>Leptonemaster</i>
	Comactiniinæ
<i>Comatula</i>	<i>Cominia</i>
<i>Comatulella</i>	<i>Comactinia</i>
	Comasterinæ
<i>Comaster</i>	<i>Comanthina</i>
<i>Comantheria</i>	<i>Comanthus</i>
	Heliometrinæ
	<i>Promachocrinus</i>
	Plicatocrinidæ
	<i>Ptilocrinus</i>

2. *One or More Rays Dwarfed, or Enlarged*

Geographical Distribution.—

Malayan region and north Australia, and Caribbean Sea, but only in warm and shallow water; Malay Archipelago to southern Japan, and Galápagos Islands to Central America in deep cold water.

Systematic Distribution.—

	Capillasterinæ
	<i>Capillaster</i> (part)
	Comactiniinæ
	<i>Comatula</i>
	Comasterinæ
<i>Comaster</i> (part)	<i>Comanthina</i>

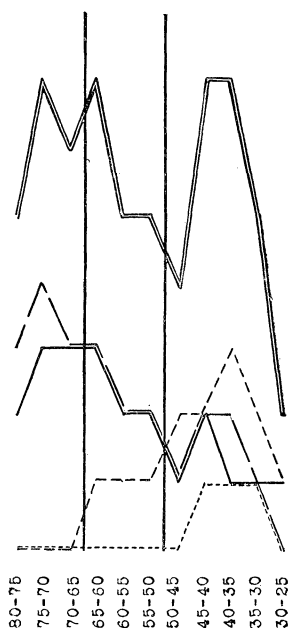


FIG. 5. Frequency at Different Temperatures of Families including Species in which the Disk is not Radially Symmetrical (—), Families including Species with one or More Rays Dwarfed or Enlarged (— — —), Families including Species with from Six to Ten Rays (---), and Families including Species with Three Basals (.....), and the Total of all these Irregularities.

Comantheria (part)*Comanthus* (part)

Apiocrinidæ

*Proisocrinus**Carpenterocrinus*

Holopodidæ

Holopus

Plicatoocrinidæ

Calamocrinus

3. Six to Ten (Sometimes Four) Rays

Geographical Distribution.—Southern Japan and the Hawaiian Islands to the Malay Archipelago, in rather deep water; abysses of the Indian Ocean and the Antarctic; Florida northward and northeastward to Iceland and Norway in deep and cold water.



FIG. 6. Proportion at Different Depths of Genera only Symmetrical Species, and Genera including Species with Asymmetrical Disks (————), Genera including Species with One or More of the Rays Dwarfed or Enlarged (— — —), Genera including Species with from Six to Ten Rays (— · —), and Genera including Species with Three Basals (· · · · ·).

This feature as an individual variant occurs in the warm water of the Malayan region, in the shallower portions of the Caribbean Sea, and very commonly on the tropical Brazilian coast.

Depth (Fathoms)	Disk Not Radially Sym- metrical (17)	One or More Rays Dwarfed or Enlarged (10)	Six to Ten Rays (4)	Three Basals (4)	Total (35)
0-50	(15) 88	(7) 70	(1) 25	0	(23) 66
50-100	(13) 76	(6) 60	(2) 50	0	(21) 60
100-150	(11) 65	(4) 40	(2) 50	0	(17) 49
150-200	(9) 53	(2) 20	(2) 50	0	(13) 37
200-250	(4) 23	0	(2) 50	0	(6) 17
250-300	(4) 23	0	(1) 25	(1) 25	(6) 17
300-350	(2) 12	0	(1) 25	(1) 25	(4) 11
350-400	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
400-450	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
450-500	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
500-550	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
550-600	(2) 12	(2) 20	(2) 50	(1) 25	(7) 20
600-650	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
650-700	(2) 12	(1) 10	(3) 75	(1) 25	(7) 20
700-750	(2) 12	(1) 10	(3) 75	(1) 25	(7) 20
750-800	(2) 12	(1) 10	(3) 75	(1) 25	(7) 20
800-850	(2) 12	0	(3) 75	(1) 25	(6) 17
850-900	(1) 6	0	(3) 75	(1) 25	(5) 14
900-950	(1) 6	(1) 10	(3) 75	(1) 25	(6) 17
950-1,000	(1) 6	0	(3) 75	(2) 50	(6) 17
1,000-1,100	(1) 6	0	(3) 75	(2) 50	(6) 17
1,100-1,200	(1) 6	0	(3) 75	(2) 50	(6) 17
1,200-1,300	(1) 6	0	(3) 75	(2) 50	(6) 17
1,300-1,400	(1) 6	0	(2) 50	(2) 50	(5) 14
1,400-1,500	(1) 6	0	(2) 50	(2) 50	(5) 14
1,500-1,600	(1) 6	0	(2) 50	(2) 50	(5) 14
1,600-1,700	(1) 6	0	(2) 50	(3) 75	(6) 17
1,700-1,800	(1) 6	0	(2) 50	(3) 75	(6) 17
1,800-1,900	(1) 6	0	(1) 25	(3) 75	(5) 14
1,900-2,000	(1) 6	0	(1) 25	(3) 75	(5) 14
2,000-2,500	(1) 6	0	(1) 25	(3) 75	(5) 14
2,500-3,000	0	0	0	(1) 25	(1) 3

Temperature (Fahrenheit)	Disk Not Radially Symmetrical	One or More Rays Dwarfed or Enlarged	Six to Ten Rays	Three Basals	Total
80°-75°	2	3	0	0	5
75 -70	3	4	0	0	7
70 -65	3	3	0	0	6
65 -60	3	3	1	0	7
60 -55	2	2	1	0	5
55 -50	2	2	1	0	5
50 -45	1	1	2	0	4
45 -40	2	2	2	1	7
40 -35	1	2	3	1	7
35 -30	1	1	2	1	5
30 -25	1	0	1	0	2

Systematic Distribution.—

Heliometrinæ

Promachocrinus

Pentametrocrinidæ

Thaumatoocrinus

Bourguetierinidæ

Monachocrinus (part)*Rhizocrinus*

Depth (Fathoms)	Number of Genera with Asymmetrical Disks	Number of Genera with Symmetrical Disks	The Number of Genera having Asymmetrical Disks Expressed as a Percentage of the Number with Symmet- rical Disks
0-50	15	51	29
50-100	13	55	23
100-150	11	53	21
150-200	9	45	20
200-250	4	40	10
250-300	4	35	11
300-350	2	31	6
350-400	2	34	6
400-450	2	32	6
450-500	2	30	7
500-550	2	29	7
550-600	2	30	7
600-650	2	29	7
650-700	2	26	8
700-750	2	26	8
750-800	2	22	9
800-850	2	21	9
850-900	1	21	5
900-950	1	23	4
950-1,000	1	20	5
1,000-1,100	1	20	5
1,100-1,200	1	16	5
1,200-1,300	1	13	8
1,300-1,400	1	12	8
1,400-1,500	1	10	10
1,500-1,600	1	10	10
1,600-1,700	1	7	14
1,700-1,800	1	7	14
1,800-1,900	1	6	16
1,900-2,000	1	6	16
2,000-2,500	1	6	16
2,500-3,000	0	4	0

4. *Three Basals*

Geographical Distribution.—Antarctic regions, and northward to northwestern Africa, the Caroline Islands, and British Columbia, except in the antarctic always in very deep water.

Systematic Distribution.—

Plicatocrinidæ

*Ptilocrinus**Gephyrocrinus**Hyocrinus**Thalassocrinus*

The frequency of each of these four types of asymmetry at different depths and temperatures is given in the tables on page 541 and in Fig. 4.

Depth (Fathoms)	Number of Genera with Asymmetrical Rays	Number of Genera with Symmetrical Rays	The Number of Genera with Asymmetrical Rays Expressed as a Percentage of the Number with Sym- metrical Rays
0-50	7	59	12
50-100	6	62	9
100-150	4	60	6
150-200	2	52	4
200-250	0	44	0
250-300	0	39	0
300-350	0	33	0
350-400	1	35	3
400-450	1	33	3
450-500	1	31	3
500-550	1	30	3
550-600	2	30	6
600-650	1	30	3
650-700	1	27	4
700-750	1	27	4
750-800	1	23	4
800-850	0	23	0
850-900	0	22	0
900-950	1	23	4
950-1,000	0	21	0
1,000-1,100	0	21	0
1,100-1,200	0	17	0
1,200-1,300	0	14	0
1,300-1,400	0	13	0
1,400-1,500	0	11	0
1,500-1,600	0	11	0
1,600-1,700	0	8	0
1,700-1,800	0	8	0
1,800-1,900	0	7	0
1,900-2,000	0	7	0
2,000-2,500	0	7	0
2,500-3,000	0	4	0

In the table showing the frequency at different depths the numbers in parentheses represent the actual cases, the other numbers being the percentage of the total number of genera in which the feature under consideration is found. This last is given in parentheses at the head of each column.

For a graphic representation of the data in the table on the lower part of page 541 see Fig. 5.

These frequencies group themselves as follows:

80°-60°	6.2
60-45	4.7
45-30	6.3
Below 30	2.0

or, segregating those occurring at the optimum temperature:

80°-65°	6.0
65-50	5.6
50-30	5.7
Below 30	2.0

Depth (Fathoms)	Number of Genera with More Than Five Rays	Number of Genera with Always Five Rays	The Number of Genera with More Than Five Rays Expressed as a Percentage of the Num- ber with Five Rays
0-50	1	65	1
50-100	2	66	3
100-150	2	62	3
150-200	2	52	4
200-250	2	42	5
250-300	1	38	3
300-350	1	32	3
350-400	2	34	6
400-450	2	32	6
450-500	2	30	6
500-550	2	29	7
550-600	2	30	6
600-650	2	29	7
650-700	3	25	12
700-750	3	25	12
750-800	3	21	14
800-850	3	20	15
850-900	3	19	16
900-950	3	21	14
950-1,000	3	18	16
1,000-1,100	3	18	16
1,100-1,200	3	14	21
1,200-1,300	3	11	27
1,300-1,400	2	11	18
1,400-1,500	2	9	22
1,500-1,600	2	9	22
1,600-1,700	2	6	33
1,700-1,800	2	6	33
1,800-1,900	1	6	16
1,900-2,000	1	6	16
2,000-2,500	1	6	16
2,500-3,000	0	4	0

The relation at different depths between the crinoids in which the disk is not radially symmetrical and those in which it is radially symmetrical is shown in the table on page 542 and in Fig. 6.

The relation at different depths between the crinoids in which one or more rays are dwarfed, or, more rarely, enlarged, and those in which all of the rays are of the same size is shown in the table on page 543 and in Fig. 6.

Depth (Fathoms)	Genera with Three Basals	Genera with Five Basals	The Number of Genera with Three Basals Expressed as a Percentage of the Number with Five Basals
0-50	0	66	0
50-100	0	68	0
100-150	0	64	0
150-200	0	54	0
200-250	0	44	0
250-300	1	38	2
300-350	1	32	3
350-400	1	35	3
400-450	1	33	3
450-500	1	31	3
500-550	1	30	3
550-600	1	31	3
600-650	1	30	3
650-700	1	27	4
700-750	1	27	4
750-800	1	23	4
800-850	1	22	4
850-900	1	21	5
900-950	1	23	4
950-1,000	2	19	10
1,000-1,100	2	19	10
1,100-1,200	2	15	13
1,200-1,300	2	12	16
1,300-1,400	2	11	18
1,400-1,500	2	9	22
1,500-1,600	2	9	22
1,600-1,700	3	5	60
1,700-1,800	3	5	60
1,800-1,900	3	4	75
1,900-2,000	3	4	75
2,000-2,500	3	4	75
2,500-3,000	1	3	33

The relation at different depths between the crinoids with more (less frequently less) than five rays, and those with five rays, is shown in the table on page 544 and in Fig. 6.

The relation at different depths between the crinoids with three basals and those with five is given in the table given above and in Fig. 6.

SUMMARY

Among the recent crinoids any wide departure from the normal close approximation to true pentamerous symmetry indicates unfavorable conditions of one or other of two main types, which are not mutually exclusive.

These two types are

1. INTERNAL UNFAVORABLE CONDITIONS, induced by incipient phylogenetical degeneration through type-senescence, as in the Plicatocrinidæ, which in the recent seas represent the almost exclusively palæozoic Inadunata; and

2. EXTERNAL UNFAVORABLE CONDITIONS, taking the form of

(a) *Phylogenetically excessive cold*, which, to cite one example, appears to be the determining factor in the asymmetry of the genus *Promachocrinus*; or of

(b) *Phylogenetically excessive warmth*, which appears to be the determining factor in the asymmetry of the family Comasteridæ.